

The meaning and consequences of foraging mode in snakes

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Introduction

We examine current knowledge of the foraging modes of snakes with particular reference to the "syndrome hypothesis" (McLaughlin, 1989) as described for other organisms. Foraging modes of snakes are often flexible, with some species exhibiting both ambush and active tactics (Hailey and Davies, 1986; Duvall *et al.*, 1990; Greene, 1997; see Table 11.1). In this chapter we focus on inter-specific comparisons and broad-scale patterns among snakes; intraspecific variation in foraging mode is considered elsewhere (Shine and Wall, this volume, Chapter 6). In general, we find some evidence that snakes exhibit variation that is broadly consistent with the syndrome hypothesis. However, physiological and morphological data are scant, and phylogenetic relationships are poorly known. In addition, we question the criteria for defining foraging modes among snakes, and the dichotomous descriptive classification of snakes into "ambush" or "active" modes. We present evidence from bioenergetic simulation that suggests these dichotomous classes may be adaptive peaks; however, intermediate trait values are certainly attainable under permissive circumstances.

How are snakes different from lizards?

All snakes are carnivorous, gape-limited predators that swallow food whole. Therefore, snakes must supply energy to a relatively large body mass by ingesting potentially large prey through a relatively small mouth (Greene, 1997). The squamate reptile skull has evolved greatly from a relatively rigid (non-kinetic) form typical of lizards to a highly modified and highly kinetic form typical of the advanced snakes (alethinophidians, Fig. 11.1) (Greene, 1997; Cundall and Greene, 2000). The scolecophidians (Fig. 11.1) are the sister

Table 11.1 *A list of North American snakes that utilize flexible foraging strategies, which apparently mix both active searching for prey and ambush tactics*

Information was obtained from recent taxonomic accounts of North American species, or from anecdotal accounts in other literature. Note that little is known about the extent to which flexible foraging tactics are used.

Family/species	Literature source
Colubridae	
<i>Elaphe obsoleta</i>	Greene, 1997
<i>Elaphe quadrivirgata</i>	Greene, 1997
<i>Elaphe vulpina</i>	Ernst and Barbour, 1989
<i>Lampropeltis calligaster</i>	Ernst and Barbour, 1989
<i>Nerodia erythrogaster</i>	Ernst and Barbour, 1989; Gibbons and Dorcas, 2004
<i>Nerodia harteri</i>	Gibbons and Dorcas, 2004
<i>Nerodia rhombifera</i>	Ernst and Barbour, 1989; Gibbons and Dorcas, 2004
<i>Nerodia sipedon</i>	Gibbons and Dorcas, 2004
<i>Nerodia taxispilota</i>	Gibbons and Dorcas, 2004
<i>Thamnophis atratus</i>	Rossman <i>et al.</i> , 1996; Lind and Welsh, 1994
<i>Thamnophis cyrtopsis</i>	Rossman <i>et al.</i> , 1996; Greene, 1997
Elapidae	
<i>Pelamis platurus</i>	Ernst, 1992
Viperidae	
<i>Agkistrodon contortrix</i>	Ernst, 1992; Greene, 1997
<i>Agkistrodon piscivorus</i>	Ernst, 1992; Hill, 2004
<i>Crotalus adamanteus</i>	Ernst, 1992
<i>Crotalus atrox</i>	Ernst, 1992
<i>Crotalus horridus</i>	Ernst, 1992 (evidence circumstantial)
<i>Crotalus mitchelli</i>	Ernst, 1992
<i>Crotalus molossus</i>	Ernst, 1992
<i>Crotalus pricei</i>	Ernst, 1992
<i>Crotalus scutulatus</i>	Ernst, 1992
<i>Crotalus tigris</i>	Ernst, 1992
<i>Crotalus viridis</i>	Ernst, 1992; Duvall <i>et al.</i> , 1990
<i>Crotalus willardi</i>	Ernst, 1992
<i>Sistrurus miliarius</i>	Ernst, 1992

group to Alethinophidians and most likely the oldest extant lineage of snakes (Greene, 1983). Scolecophidians are typically fossorial and secretive, feeding on small invertebrates (Greene, 1983, 1997; Cundall and Greene, 2000). The skull of the Scolecophidia is compact, with short mandibles and limited maxillary and mandibular movement (Cundall and Greene, 2000). The relatively non-kinetic skull and short mandibles of the scolecophidians results in a small gape relative to macrostomates (Cundall and Greene, 2000) (Fig. 11.1). In a progression from

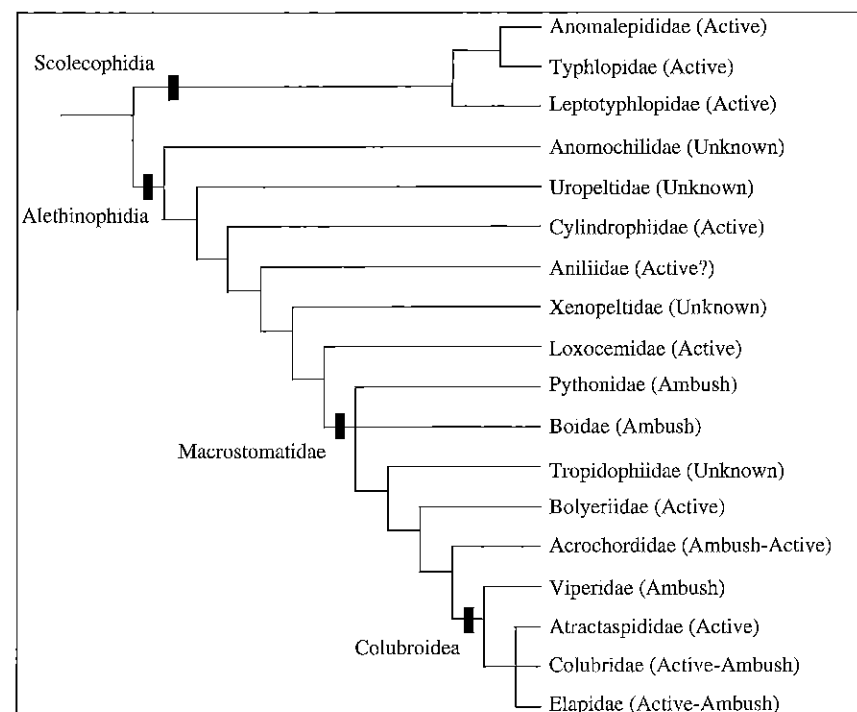


Figure 11.1. Hypothesized phylogenetic relationships of the familial relationships of snakes (redrawn from Cundall and Greene, 2000). Origin in an active foraging varanoid ancestor is assumed. Predominantly ambush foraging lineages are indicated in gray print. Information on foraging mode is scarce or non-existent for many families. Our assignment of foraging modes to families is based on a combination of literature information (Greene, 1997; Zug *et al.*, 2001), and on consultation with experienced individuals. We note that Acrochordidae in particular have been described as active searchers for sleeping fish (Houston and Shine, 1993) and as ambush foragers (H.B. Lillywhite, pers. comm.). Reversals and foraging mode flexibility are discussed in more detail in the text, and indicated in Table 11.1, respectively. For those taxa where both active and ambush are indicated, we list the predominant mode first, and list the alternative second because of known exceptions (Table 11.1, and see text).

the basal alethinophidians to the Macrostromata, there is an increase in the kinesis of the skull, and an increase in mandible length, allowing increased gape size (Cundall and Greene, 2000). The Colubroidea (Fig. 11.1) exhibit highly kinetic skulls, and include all venomous taxa (Cundall and Greene, 2000). An evolutionary trend of increasing skull kinesis and maxillary liberation is coincident with the impressive radiation within Colubroidea and the diverse feeding adaptations found therein (Cundall and Greene, 2000).

Along with increased gape, allowing for larger prey to be ingested, snakes have evolved more diverse modes of prey subjugation than those found among lizards. Because of the vulnerability of the head during a predatory attack on relatively large prey, more derived snakes probably assume greater risk when subduing larger, potentially dangerous prey (Cundall and Beaupre, 2001; Kardong and Smith, 2002). Snakes typically show three broad forms of prey subjugation: grasping and ingesting live, constriction, and envenomation (Greene, 1997; Cundall and Greene, 2000). Overpowering small prey and consuming it live is exhibited by many colubroid snakes; however, the prey is typically invertebrates, fish or small amphibians that have limited capacity for physical defense. For example, the turtle-headed sea snake (*Emydocephalus annulatus*) eats large numbers of small fish eggs (Shine *et al.*, 2004) and garter snakes are known for grasping and ingesting small frogs, salamanders, and their larvae alive (Rossman *et al.*, 1996). Constriction, tightening of coils around the prey resulting in respiratory and/or circulatory failure, probably arose early among alethinophidians and has been variously retained among advanced lineages (Greene, 1997). The use of envenomation in prey subjugation has evolved several times in the varanoid line: among helodermatid lizards, in the Viperidae, the Elapidae, and probably more than once in the Colubridae. Indeed, recent work isolating toxins from Asian ratsnakes (*Coelognathus radiatus*) suggests the evolution of venoms early in the radiation of the Colubroidea, implying secondary losses in several extant lineages (Fry *et al.*, 2003). Whether the system of delivery is a passive introduction of the Duvernoy's gland secretions via enlarged maxillary teeth, or active injection of venom gland secretions through hollow fangs, envenomation is a highly derived prey subjugation strategy (Cundall and Greene, 2000). Prey that are envenomated and released must be relocated in the environment, a source of selection that is probably responsible for remarkable behavioral and chemosensory adaptations that are also unique to venomous snakes (Chiszar *et al.*, 1992; Kardong and Smith, 2002).

Time-energy allocation and foraging mode

In any environment, there are a limited number of life history alternatives that will allow an organism to survive and reproduce. The number of feasible life history alternatives is limited by environmental and physiological constraints acting on three fundamental allocation decisions of life history: (i) allocation of available time to competing behaviors, (ii) allocation of available mass and energy to competing functions (maintenance, activity, growth, reproduction and storage) and (iii) the packaging of energy and mass allocated to reproduction into individual offspring (Dunham *et al.*, 1989). Animals that differ in foraging

mode also tend to differ in bioenergetic variables such as standard metabolic rate, field metabolic rate, and cost of digestion. Because both the rate at which energy and mass can be extracted from the environment, and the rate at which it is allocated to competing functions, can be expected to exert a major influence on optimal time-energy allocation, it seems reasonable that foraging mode will strongly affect the evolution of life history. As the rate of energy assimilation and cost of foraging vary with foraging mode, the allocation strategies associated with the optimal life history must also vary. Suites of traits adapted for a particular forging mode and rate of mass-energy intake are unlikely to be equally adaptive across a wide range of prey types and availability distributions.

The syndrome hypothesis

The foraging mode of an organism generally falls along a continuous spectrum between ambush foraging (sit-and-wait) and active foraging (widely foraging). However, only vague definitions for these foraging modes have been proposed. For example, ambush foragers have been defined as animals that allow potential prey to enter attack range, whereas active foragers move into attack range of potential prey (McLaughlin, 1989; Perry, 1999). In studies of lizards, foraging mode has been quantified by using mean number of movements made per minute, and percent of time spent moving (Huey and Pianka, 1981; Perry, 1999). Use of these movement data to quantify foraging mode implicitly assumes that movements relate to foraging rather than to other functions (e.g., thermoregulation, mate search, migration). Alternatively, Cooper *et al.* (1999) proposed the use of the proportion of attacks on prey discovered while lizard predators are moving in relation to total attacks made (*PAM*). Use of *PAM* carries the advantage of considering only movements specific to foraging. However, because snakes are generally secretive, and feed infrequently relative to lizards, these techniques are difficult to apply. Furthermore, ambush foraging snakes may expend considerable effort searching for high-quality ambush sites (Duvall *et al.*, 1990); such movements are rarely considered relevant when assessing foraging mode (although Greene [1992] described such animals as "mobile ambushers"). In part because of difficulties in defining foraging mode, few studies of snakes have attempted to independently characterize foraging mode when making comparisons of traits related to foraging mode among species.

Foraging mode may affect and be affected by ecological, behavioral, thermal, reproductive, and bioenergetic aspects of the life history of an organism. Commonly considered factors affecting the strategy of active vs. sit-and-wait foraging are habitat type, prey availability, type of prey, and predation

Table 11.2 Suite of characteristics associated with each extreme of the foraging mode continuum
Taken together, these trait associations have been termed the "syndrome hypothesis" (McLaughlin, 1989).

	Ambush	Active	Reference
Feeding rate	low	high	Hailey and Davies, 1986; Secor, 1995; Anderson and Karasov, 1981; Nagy <i>et al.</i> , 1984
Foraging time	long	short	Secor, 1995; Merker and Nagy, 1984
Prey type	active	active and ambush	Huey and Pianka, 1981; Naulleau and Bonnet, 1995; Secor, 1995
Diet diversity	low	high	Naulleau and Bonnet, 1995; Secor, 1995
Home range size	low	high	Secor, 1995; Naulleau and Bonnet, 1995
Movement rate/distance	low	high	Hailey and Davies, 1986; Naulleau and Bonnet, 1995; Secor, 1995; Perry, 1999
Standard metabolic rate	low	high	Fig. 11.2
Field metabolic rate	low	high	Secor and Nagy, 1994; Nagy <i>et al.</i> , 1984; Anderson and Karasov, 1981; Bennett and Gorman, 1979; Fig. 11.3
Water flux rate	low	high	Secor, 1995
Specific dynamic action	high	low	Secor and Diamond, 2000; Secor, 2001
Endurance	lower	higher	Ruben, 1976
Thermal performance	high	low	Secor, 1995
Breadth			
Growth rate and maturation	slow	fast	Webb <i>et al.</i> , 2003
Relative clutch mass	high	low	Vitt and Congdon, 1978; Huey and Pianka, 1981; Vitt and Price, 1982
Morphology	stout	slim	Vitt and Congdon, 1978; Huey and Pianka, 1981; Secor, 1995; Figs. 11.4 and 11.5
Predation risk	low	high	Secor, 1995; Bonnet <i>et al.</i> , 1999; Webb <i>et al.</i> , 2003
Predator avoidance strategy	crystis	speed	Huey and Pianka, 1981; Secor, 1995

risk associated with moving, among others (Norberg, 1977; Janetos, 1982). Previous studies (Table 11.2) suggest that widely foraging animals have more encounters with prey, a more generalist diet, higher field metabolic rates, greater water flux, lower relative clutch size, and more streamlined morphology than ambush foragers (Vitt and Congdon, 1978; Huey and Pianka, 1981; Secor and Nagy, 1994; Secor, 1995) and typically forage for a shorter period (Merker and Nagy, 1984; Nagy *et al.*, 1984). The correlation of a particular suite of characteristics with the active foraging mode and the opposite characteristics with the ambush foraging mode has been termed the "syndrome hypothesis" (McLaughlin, 1989) (Table 11.2). Here, we examine available data for snakes, and where possible assess support for the syndrome hypothesis.

Data quality and availability

We reviewed publications concerning foraging mode in snakes and examined data on morphological and physiological correlates of foraging mode. We were impressed by several shortcomings of the available data.

1. Snake researchers lack a clear definition of foraging mode that is independent of the syndrome hypothesis. Without clear and objective (repeatable) definitions of foraging modes, researchers resort to examination of syndrome-related variables to categorize organisms. At best, this practice risks circularity, and renders tests of the syndrome hypothesis suspect.
2. There is a lack of hard data with which to assess foraging mode in snakes. Usually, assignment of foraging mode is made by assertion after brief observation, after consultation with an expert, or by familial/phylogenetic association. Lack of data, coupled with ambiguous criteria for assigning foraging mode, leads to subjectivity, which will no doubt interfere with clarity in hypothesis testing.
3. Poor or incomplete data for the "syndrome." In many cases, only a single syndrome-related variable (e.g. standard metabolic rate, *SMR*, or length-mass relationship) has been measured, hampering our ability to assess the syndrome hypothesis as a whole.
4. Troubles with the adjustment of physiological variables for body size in comparative studies. Often, physiological variables (e.g. *SMR*; field metabolic rate, *FMR*) have been adjusted for body mass by generating a mass-specific ratio (i.e. kJ g^{-1}). Mass-specific ratios correct for body mass only when the relationship between mass and response is isometric (exponential slope = 1, intercept = 0), a condition rarely, if ever, met in physiological data, which typically scale allometrically (Packard and Boardman, 1988, 1999; Hayes, 2001). Rampant use of mass-specific ratios poses a major problem for comparative studies of animals that differ in

body size. Such comparisons are best accomplished by using allometric scaling relations ($Y = aX^b$), which minimize error (Packard and Boardman, 1988, 1999; Hayes, 2001).

5. The phylogenetic relationships of advanced snakes, especially the Colubroidea, are uncertain (Cundall and Greene, 2000). Most specifically, the family Colubridae may be paraphyletic, consisting of numerous lineages of uncertain placement (Cadle, 1994; Vidal and Hedges, 2002). Phylogenetic research among major groups is active, including New World Crotalinae (Parkinson, 1999; Schuett *et al.*, 2002), Elapidae (Keogh, 1998), and Colubroidea (Vidal and Hedges, 2002). However, a complete understanding of major lineages within families remains elusive and information regarding branch lengths commonly required for phylogenetic correction is available for only some groups.
6. Among snakes, there are apparently few clearly documented reversals of foraging mode within families, which hampers independent tests of correlated evolution of foraging mode and "syndrome" responses. Furthermore, many snakes defy classification into dichotomous foraging mode because of their natural flexibility in foraging tactics. Some species that belong to families that exhibit predominantly one foraging mode have been described as using alternative foraging tactics (Table 11.1) (Lind and Welsh, 1994; Fitzgerald *et al.*, 2004; Shine and Wall, this volume, Chapter 6). These snakes cannot be classified unambiguously, because they utilize both strategies, and the extent to which alternative strategies are used remains unknown.

Our discussion of the syndrome hypothesis is necessarily constrained, given the above shortcomings of available data. Below, we discuss in turn the phylogenetic, ecological, physiological, and morphological implications of foraging mode in snakes. We review relevant studies and summarize existing data in an attempt to represent the current state of understanding of foraging mode and its consequences in snakes.

Phylogenetic implications

Shifts in foraging mode within individuals have been observed in the field or induced experimentally in representatives of a number of lineages including scolopendrid centipedes, aquatic invertebrates, spiders, insects, fish, turtles, amphibians, birds, and mammals (Ehlinger, 1989; Helfman, 1990; Fausch *et al.*, 1997). However, in squamate reptiles, foraging mode is thought to be phylogenetically stable and relatively conserved within families (McLaughlin, 1989; Perry, 1999). Nevertheless, species within several squamate lineages exhibit foraging modes atypical of their families. Lineages containing reversals include but are not limited to the scincid genus *Mabuya* (Cooper and Whiting,

2000), the family Lacertidae (Huey *et al.*, 1984), geckos (Huey and Pianka, 1981; see Perry, 1999 for other lizard examples), the Colubridae (Hailey and Davies, 1986; Daltry *et al.*, 2001), and Australian elapid snakes (Shine, 1980; Webb *et al.*, 2003). A shift from active to ambush foraging is thought to be more likely than a shift from ambush to active foraging owing to the physiological constraints (e.g. cost of locomotion, endurance, aerobic capacity) operating on heavy-bodied ambush foragers (Huey and Pianka, 1981). Assuming that snakes evolved from active-foraging varanoid lizards, it is likely that ambush foraging has evolved several times, most notably among Boidae and Viperidae (Fig. 11.1).

Within the Serpentes the stability of predominant foraging mode within families is perhaps more highly conserved than in lizards. Again, some exceptions (reversals) exist. Within the family Elapidae, the death adder (*Acanthophis* sp.) is convergent on the body form and foraging mode of terrestrial viperids (Shine, 1980), and the broad-headed snake (*Hoplocephalus bungaroides*) is an ambush forager that exhibits some evidence of directional evolution in life history traits towards those more typical of pit-vipers (Webb *et al.*, 2003). Furthermore, within the family Colubridae there are three well-studied reversals. Adult *Natrix maura* are ambush foragers on fish (Hailey and Davies, 1986) which is atypical of the genus *Natrix*. The Antigua racer (*Alsophis antiguae*) ambushes small lizards from the concealment of leaf litter (Daltry *et al.*, 2001). The Oregon gartersnake (*Thamnophis atratus hydrophilus*) exhibits an ontogenetic shift in foraging mode with neonates using ambush tactics, adults using active foraging, and juveniles exhibiting both modes (Lind and Welsh, 1994). Unfortunately, few syndrome-related data are available for these reversals, making detailed analysis of trait evolution impracticable for these cases. Owing to the highly conserved nature of foraging mode within taxonomic groups, and the lack of specific knowledge regarding foraging mode and phylogeny, it is difficult to find circumstances that allow comparisons of behavior, physiology, and morphology between alternative foraging modes in sympatric, closely related snakes.

Ecological implications

The syndrome hypothesis includes a number of ecological characters that are associated with foraging mode (Table 11.2). Active foragers show increased movement rates relative to ambush foragers (as indicated by the use of movements per minute (MPM) to quantify foraging mode in lizards). The actively foraging coachwhip, *Masticophis flagellum*, moved more than twice as frequently and greater than twice as far as the sympatric ambush foraging

sidewinder, *Crotalus cerastes* (Secor, 1995). The activity range of *M. flagellum* was also greater than twice that of *C. cerastes*, although snake size was not accounted for (Secor, 1995). In a comparison of two closely related natricine snakes, the active foraging *Natrix natrix* was active more often than the ambush foraging *N. maura* (Hailey and Davies, 1986). Likewise, the ambush foraging terrestrial asp viper (Viperidae: *Vipera aspis*) and the active foraging semi-arboreal Aesculapian snake (Colubridae: *Elaphe longissima*) differ in activity level and home range size, consistent with expectations based on foraging mode (Naulleau and Bonnett, 1995).

Diet and feeding rates

Active foragers are thought to have a more diverse diet (Secor, 1995) and to encounter prey and feed more frequently (Anderson and Karasov, 1981; Andrews, 1984; Nagy *et al.*, 1984) than ambush foragers. The difference in diet diversity is partly due to active foragers encountering both sedentary and active prey, whereas ambush foragers will encounter predominantly active prey (Huey and Pianka, 1981; McLaughlin, 1989). For example, in a study of predators on active and ambush lizards, *Bitis caudalis* (an ambush forager) fed on an active foraging lizard more often than would be expected by chance (Huey and Pianka, 1981). In addition, *Masticophis flagellum* fed twice as often, on a more diverse diet (nestling birds, snakes, lizards and mammals), as the ambush foraging *Crotalus cerastes* (mammals and lizards) (Secor, 1995). The ambush foraging *Natrix maura* fed less frequently on more active prey than the sympatric, con-generic, active foraging *Natrix natrix* (Hailey and Davies, 1986). The active foraging *Elaphe longissima* consumed birds, bird eggs, and small mammals, whereas the ambush foraging *Vipera aspis* consumed only small mammals (Naulleau and Bonnet, 1995). A potential relationship between foraging mode and prey size is complicated by changes in prey geometry (Cundall and Greene, 2000). For example, pit-vipers (primarily ambush foragers) take prey that may exceed 160% of their body mass (Greene, 1992). Actively foraging coral snakes (*Micrurus fulvius*) may take meals of nearly equal proportion (137%) by mass (Greene, 1997); however, large meals in ophiophagous and saurophagous coral snakes are facilitated by the cylindrical body form of snakes and lizards. In addition, some active foragers (e.g. turtle-headed sea snakes, *Emydocephalus annulatus*; Shine *et al.*, 2004) feed on large numbers of small prey, which may result in relatively large total meal sizes. However, there is no direct evidence for prey size selectivity between ambush foraging and active foraging snakes (Downes, 2002).

Predation risk

Ambush foragers rely on crypsis and a sedentary lifestyle to avoid predation; active foragers are more visible to predators, since they show greater activity, and must flee from potential predators (Huey and Pianka, 1981). Therefore, the active foraging lifestyle carries a greater risk of predation (Huey and Pianka, 1981; Webb *et al.*, 2003). In a study relating activity to road mortality in four snake species, active foraging snakes were killed more often than ambush foragers (Bonnet *et al.*, 1999). Juvenile survival was much greater in the ambush foraging *Hoplocephalus bungaroides* when compared with the active foraging *Rhinoplocephalus nigrescens* (Webb *et al.*, 2003). However, adult survival was similar in these species, possibly because of increased risk during extensive summer movements by ambush foraging *H. bungaroides* (Webb *et al.*, 2003). Active foraging *Masticophis flagellum* was depredated twice as often as ambush foraging *Crotalus cerastes* over a three-year period (Secor, 1995).

Relative clutch mass

The syndrome hypothesis suggests that active foragers should have a lower relative clutch mass (*RCM*) than ambush foragers (Vitt and Congdon, 1978; Vitt and Price, 1982). Lower *RCM* in active foragers may result, in part, from lower maternal body volume available for developing offspring, owing to the decreased mass – *SVL* relation. In addition, increased *RCM* results in greater total mass being transported by the mother during pregnancy or gravidity, which would result in a greater energetic cost of locomotion. Cost of transport for greater body mass may hinder escape from potential predators and therefore increase predation risk to the mother (Vitt and Congdon, 1978); this probably influences active foragers far more than sedentary ambush foragers, which rely heavily on crypsis. Unfortunately, *RCM* is computed by generating a ratio of clutch or litter mass to maternal mass. Such ratios assume isometric scaling between ratio components, a condition that is rarely met when considering body size. As previously mentioned, the use of simple ratios to represent allometric relations and to statistically compare groups that differ in body size has been criticized (Packard and Boardman, 1988, 1999). Such comparisons are subject to estimation errors and spurious correlations. In addition, *RCM* is sensitive to resource environment because clutch or litter size are sensitive to resource environment, and at least some low-energy specialists (e.g. rattlesnakes) frequently produce litters that are well below their capacity (S. Beaupre, personal observation). Finally, a comparison of *RCM* between foraging modes would be partly confounded by reproductive mode (oviparity,

viviparity). The majority of Viperidae are viviparous, whereas most Elapidae and Colubridae are oviparous. Because of problems with the statistical comparison of *RCM* among groups that differ in size, the variable nature of *RCM*, and the complexity of dealing with confounding factors such as reproductive mode, we did not pursue comparisons of *RCM* between active and ambush foraging snakes. Such an analysis is beyond the scope of the current chapter.

Physiological implications

Fundamental constraints dictated by the laws of thermodynamics set bounds on the evolution of life history (Dunham *et al.*, 1989). Survival, growth and reproduction require energy intake (Bryant, 1988); thus, it is reasonable that aspects of digestive and metabolic physiology should be finely tuned to optimize net energy gain in response to feeding rates and food volumes associated with different foraging modes. Such tuning may not be in direct response to foraging mode *per se*, but rather to a suite of variables that may or may not covary with foraging mode such as feeding frequency (Secor and Diamond, 2000), prey size (Forsman and Lindell, 1993) and prey abundance (Forsman and Lindell, 1997). For example, three large ambush foraging radiations of snakes (boas, pythons, and pit-vipers) have also been described as “low-energy” systems because of comparatively low metabolic rates (Chappell and Ellis, 1987; Beaupre 1993; Beaupre and Duvall, 1998; Beaupre and Zaidan, 2001), relative to active foraging colubrids and lizards. Major bioenergetic features that appear to be sensitive to foraging mode (and related variables) include standard metabolic rates, field metabolic rates, and the magnitude of the cost of digestion (specific dynamic action: *SDA*). We consider each of these in turn.

Metabolism

Energy allocation to standard or resting metabolic rate can account for a sizeable portion of the total annual energy budget in snakes: 20%–30% in *Crotalus lepidus* depending on source population (Beaupre, 1996), approximately 30% in *Crotalus cerastes*, and 23% in *Masticophis flagellum* (Secor and Nagy, 1994). Therefore, reductions in *SMR* can result in significant energy savings when accumulated over the course of several months.

Metabolic rate is affected by abiotic (temperature, time of day, season) and biotic factors (body size, reproductive condition, digestive status) and therefore comparisons among taxa must be made at common values of these factors. Although the allometry between body size and metabolic rate has

been established in reptiles (Andrews and Pough, 1985) including rattlesnakes (Beaupre, 1993; Beaupre and Duvall, 1998; Beaupre and Zaidan, 2001), colubrids (Peterson *et al.*, 1998), and boids (Chappell and Ellis, 1987), a large proportion of researchers still report metabolic rates in mass-specific form (e.g. $\text{kJ g}^{-1} \text{h}^{-1}$ or $\text{ml O}_2 \text{g}^{-1} \text{h}^{-1}$). As mentioned above, use of ratios that assume isometry with variables that are allometrically related will induce error in comparative studies (Packard and Boardman, 1988, 1999). The preponderance of mass-specific metabolic rates in the literature poses a problem for the comparison of standard and resting metabolic rates between snakes that differ in foraging mode and body size.

Nevertheless, the metabolism of several snakes has been examined in comparisons of the costs and benefits of foraging mode. For example, the ambush foraging vipers *Vipera berus* and *Cerastes cerastes* exhibited significantly lower resting metabolic rate (*RMR*) than the actively foraging colubrid *Malpolon moilensis* (Al-Sadoon, 1991). The actively foraging colubrid *Natrix natrix* had greater aerobic scope at high temperatures than ambush foraging *N. maura* (Hailey and Davies, 1986). The actively foraging coachwhip (Colubridae: *Masticophis flagellum*) had significantly greater *RMR* and field metabolic rate (*FMR*) in comparison with the sit-and-wait foraging sidewinder (Viperidae: *Crotalus cerastes*) (Secor and Nagy, 1994; Secor, 1995). Likewise, in a comparison of metabolic rate between the ambush foraging prairie rattlesnake (Viperidae: *Crotalus viridis*), the active foraging racer (Colubridae: *Coluber constrictor*) and coachwhip (Colubridae: *Masticophis flagellum*), and the ambush foraging rosy boa (Boidae: *Lichanura roseofusca*), no differences were found in *SMR*; however, the active foragers had higher rates of metabolism during physical activity (Ruben, 1976). In general, resting and standard metabolic rates are thought to be greater in active foragers relative to ambush foragers.

To further evaluate the relationship between foraging mode and metabolic rate, we collated literature values of *SMR* for both active and ambush foraging snakes. We limited our analysis to only those studies where data were available to estimate metabolic rate at 30°C, and where either an allometric scaling equation or a mass-specific rate (along with an average mass of the animals studied) was reported (Data: Appendix 11.1). We estimated whole animal metabolic rate for an animal of average body mass for the species by using an allometric relation, or for the average sample body mass of animals measured when given a mass-specific rate. Using the average mass of the sample is the best approach when the *SMR* is reported on a mass-specific basis because, even though the allometric relation is not known, the whole animal estimate should be accurate at the average sample mass. When available, and clearly defined by the investigators, we used estimated *SMR*; otherwise we used the lowest

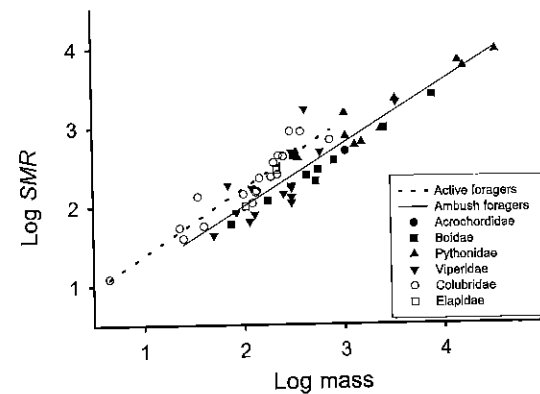


Figure 11.2. Comparisons of *SMR* between ambush and active foraging snakes. Standard metabolic rates were obtained from literature accounts and converted to a mean value for each represented species as a function of mean species or sample body size (see text for details).

metabolic rates measured and took these to be a reasonable estimate of *SMR*. All *SMR* values were converted to common units (kJ h^{-1}) by using conversion factors supplied by Gessaman and Nagy (1988). We used ANCOVA (Fit Model Platform, JMP ver 5.1, 2003, SAS Institute, Cary, NC) to assess the effects of body mass and foraging mode on *SMR* (model: $\text{LogSMR} = \text{LogMass}$, Mode, $\text{LogMass} \times \text{Mode}$) on 56 observations of *SMR* from the literature.

As expected, body mass significantly affected *SMR* ($\text{df} = 1$, $F = 213.6$, $p < 0.0001$; Fig. 11.2) as did foraging mode ($\text{df} = 1$, $F = 10.7$, $p < 0.0019$; Fig. 11.2). Furthermore, the slope of the relation between body mass and *SMR* was similar between active and ambush foragers ($\text{df} = 1$, $F = 0.19$, $p < 0.6623$; Fig. 11.2). The above model explained 87.2% of the variation in the dataset. At face value, this analysis supports the notion that active foraging snakes have higher *SMR* than ambush foraging snakes. However, we note that an appropriate phylogenetic correction should first be applied. We did not pursue phylogenetic correction in this analysis because foraging mode and family are completely confounded (i.e. nearly all Colubridae in the sample are active, all Viperidae are ambush, all Boidae are ambush) and the phylogenetic relationships of these groups are poorly known. To illustrate the confounding of family and foraging mode, we ran a second analysis with the model: $\text{LogSMR} = \text{LogMass}$, Family, $\text{LogMass} \times \text{Family}$. The elapids ($n = 2$) and our single acrochordid were dropped from the analysis because of lack of replication at the family level, resulting in four remaining families for comparison (Boidae, Pythonidae, Colubridae, and Viperidae). In this case again, body mass significantly affected *SMR* ($\text{df} = 1$, $F = 203.1$, $p < 0.0001$) as did family

($df = 1$, $F = 4.1$, $p < 0.0121$), and the slope of the relation between body mass and SMR was similar among families ($df = 3$, $F = 0.63$, $p < 0.5991$). Body mass and family also explained 87.2% of the variation in SMR . Based upon current data, standard metabolic rates of active foraging snakes appear to be significantly elevated relative to ambush foraging snakes, but this effect cannot be cleanly attributed to foraging mode because of the confounding influence of family membership. However, we urge caution in the interpretation of our SMR analysis, because species most likely differ in their allometric relations between SMR and body mass, and little scaling information was available to us (because of pervasive reporting of mass-specific rates).

Field metabolic rate

Field metabolic rates (FMR) using the doubly labeled water method have been infrequently measured in snakes. However, there are several instances of measurement within Colubridae (*Masticophis flagellum*, Secor and Nagy, 1994; *Coluber constrictor*, Plummer and Congdon, 1996; *Thamnophis sirtalis*, Peterson *et al.*, 1998), and several within Viperidae (*Crotalus atrox*, S. Beaupre *et al.*, in prep; *Crotalus cerastes*, Secor and Nagy, 1994; *Crotalus horridus*, S. Beaupre, in prep; *Crotalus lepidus*, Beaupre, 1996). We present these values as a combination of regression lines (when scaling relations were available) and as whole-animal responses vs. mean body mass of the sample when only mass-specific rates were available (Fig. 11.3). Clearly, active foragers in the sample (*C. constrictor*, *M. flagellum*, and *T. sirtalis*) have elevated FMR relative to ambush foragers (*C. atrox*, *C. cerastes*, *C. horridus*, and *C. lepidus*). However, in this case there are only two families represented, and again, foraging mode is completely confounded with family membership. Furthermore, *Masticophis* and *Coluber* are thought to be closely related, and all of the vipers represented are from a single genus. Nevertheless, variation in FMR in relation to foraging mode in snakes measured to date is consistent with the syndrome hypothesis.

Specific dynamic action

Specific dynamic action (SDA) is defined as the cost of digestion and includes energy expenditures associated with intestinal up-regulation and growth, active transport, peristalsis, intermediary protein metabolism, and synthesis associated with the processing of a meal. In a comparison of ambush foraging *Crotalus cerastes* and active foraging *Masticophis flagellum*, Secor and Nagy (1994) and Secor *et al.* (1994) noted that the SDA of the ambush foraging

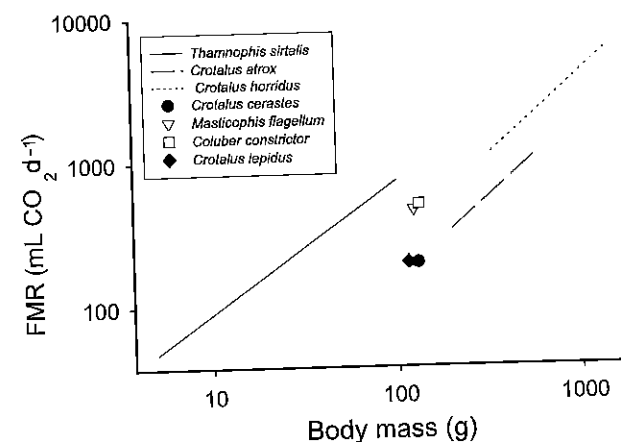


Figure 11.3. Field metabolic rates (FMR) in the form of allometric relations or point estimates for small samples where allometric relations were not available. Ambush foraging snakes tend to exhibit lower FMR than active foragers; however, comparisons are completely confounded by family membership (see text for details).

rattlesnake was much greater than that of the widely foraging coachwhip. The factorial increase in metabolic rate due to SDA ranged as much as 6.6-fold in *C. cerastes* (Secor *et al.*, 1994) and only 3.7-fold in *M. flagellum* (Secor and Nagy, 1994). Secor and Diamond (2000) have since developed the hypothesis that feeding frequency drives the evolution of gut function, such that infrequent feeding (typical of ambush foragers) selects for down-regulation of gut function during fasting periods to reduce whole-animal metabolic costs (with concurrent high cost of SDA due to added need for up-regulation upon feeding). Conversely, frequent feeding (typical of active foragers) selects for constant readiness of the gut to process food, resulting in higher whole-animal metabolic rates and lower costs of SDA . Additional data, including phylogenetically corrected comparative analyses (Secor and Diamond, 2000; Secor, 2001; Zaidan and Beaupre, 2003) support the contention that the magnitude of SDA is related to feeding frequency (hence, indirectly to foraging mode), and that infrequent feeders examined had SDA that was approximately 1.8 times greater than the SDA of frequent feeders (Secor and Diamond, 2000).

Morphological implications

Morphological variation also appears to be related to foraging mode in snakes. Active foragers typically have a more streamlined body form, generally

expressed as a lower mass to snout-vent length (*SVL*) relation, and a higher tail length to snout-vent length relation compared with ambush foragers (Vitt and Congdon, 1978). Foraging mode, specifically movement rates, may constrain body form. Active foragers typically exhibit greater movement rates (Perry, 1999) and higher metabolic cost of searching for prey relative to ambush foragers (Nagy *et al.*, 1984). The energetic cost of locomotion increases with an increase in the mass being moved, all other things being equal. The observation that active foragers have less mass at a given body length (Vitt and Congdon, 1978) is consistent with the prediction that active foragers should reduce total cost of transport.

Mass-length relations can be used to compare among diverse taxa that differ in foraging mode. We searched the snake literature for mass-length allometric equations or data from which such allometric equations could be generated. We found ample data for snakes in three families: Colubridae (Kaufman and Gibbons, 1975; A. T. Holycross, unpublished data, 2003), Elapidae (Greer and Shine, 2000), and Viperidae (Kaufman and Gibbons, 1975; A. T. Holycross, unpublished data, 2002; J. Hobert, unpublished data, 2002; S. J. Beaupre, unpublished data, 2002; S. J. Beaupre and C. E. Montgomery, unpublished data, 2003; J. G. Hill, unpublished data, 2003; F. Zaidan, unpublished data, 2002). For each species, we obtained or generated a scaling relationship of the form: $Mass = aSVL^b$ where mass is in grams, *SVL* is snout-vent length (cm), and *a* and *b* are fitted constants, hereafter referred to as intercept and exponent, respectively. In general, larger *a* values correspond to fatter animals per unit length. Larger *b* values imply a faster increase in mass with increasing length, but this would most reliably correspond to fatter animals per unit length if *a* values were similar between taxa, or larger in the fatter taxon. If the syndrome hypothesis is correct, we predicted that ambush foraging snakes (Viperidae) could have greater intercept and/or exponent values, indicating greater body mass at a given length or faster increase in mass with increases in length. To test this hypothesis, we plotted each species in two-dimensional space represented by values of *a* and *b*, and examined the result for structure. We noted non-linearity and log-transformed both variables. Mass-length relations group with family; ambush foraging Viperidae exhibit greater values of log *a* at a given value of log *b* (Fig. 11.4) and greater values of log *b* at a given value of log *a*, both of which suggest larger mass at length among the Viperidae. To examine this pattern for statistical significance, we conducted ANCOVA (model $\log a = \log b$, family, $\log b \times \text{family}$). We found significant effects ($r^2 = 0.954$) of log *b* ($df = 1$, $F = 369.1$, $p < 0.0001$) and family ($df = 2$, $F = 14.8$, $p < 0.0001$) on log *a*. Furthermore, the log *b* \times family interaction was non-significant ($df = 2$, $F = 0.97$, $p < 0.3898$), indicating parallel slopes

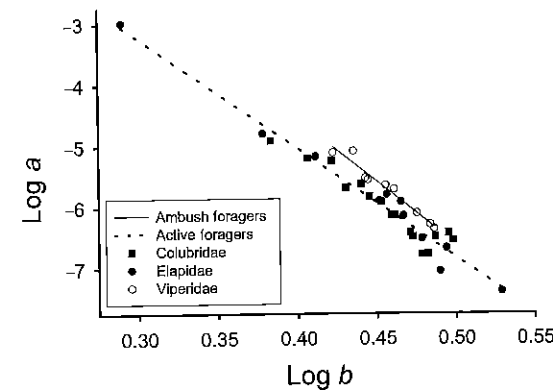


Figure 11.4. Morphological comparison among families. Allometric relations of *SVL* and body mass of the families Colubridae, Elapidae, and Viperidae (see text for data sources). The pattern of a decrease in mass to *SVL* relation in active foragers is apparent, suggesting relatively thinner body form. However, comparisons are again confounded by familial membership.

among families. The Viperidae were significantly different from Colubridae and Elapidae (by Tukey's HSD; $p < 0.05$). A family effect, with ambush foraging Viperidae exhibiting greater mass at length, is consistent with the syndrome hypothesis. Because foraging mode and family were confounded in this analysis, the same amount of variance ($r^2 = 0.955$) was explained when mode was substituted for family.

If morphology evolves in response to foraging mode, then it is reasonable to expect that snakes within a predominantly ambush foraging family (e.g. Viperidae) that exhibit more active foraging might also exhibit evolution towards more slender body form. For example, within North American crotalines the copperhead, *Agkistrodon contortrix*, has a significantly different relation between body mass and *SVL* when compared with most other crotalines (Fig. 11.5). Raw data (*SVL* and body mass) were available for ten species (*Agkistrodon piscivorus*, F. Zaidan, unpublished data, 2002; *Crotalus atrox*, S. J. Beaupre, unpublished data, 2002; A. T. Holycross, unpublished data, 2002; *Crotalus horridus*, S. J. Beaupre, unpublished data, 2002; *Crotalus lepidus*, S. J. Beaupre, unpublished data, 2002; A. T. Holycross, unpublished data, 2002; *Crotalus molossus*, S. J. Beaupre, unpublished data, 2002; A. T. Holycross, unpublished data, 2002; *Crotalus scutulatus*, A. T. Holycross, unpublished data, 2002; *Crotalus viridis*, A. T. Holycross, unpublished data, 2002; *Crotalus willardi*, A. T. Holycross, unpublished data, 2002; *Sistrurus catenatus*, A. T. Holycross, unpublished data, 2002; J. Hobert, unpublished data, 2002; and *Agkistrodon contortrix*, C. E. Montgomery and S. J. Beaupre,

Bioenergetic modeling

It is tempting to force organisms into the dichotomous extremes of active or ambush foraging. However, it may be more reasonable to think of foraging mode as a flexible continuum where, under the right circumstances, organisms could successfully exhibit phenotypes intermediate between the extremes represented by the dichotomy (Perry, 1999). It is reasonable then to ask: what are the fitness consequences of intermediate phenotypes, and what is the relative disadvantage of adopting one strategy in an environment that best supports the other? Such questions are difficult, at best, to answer in the field. However, bioenergetic simulations may provide some insight.

The first author has developed a bioenergetic simulation of growth and reproduction based on data from ambush foraging rattlesnakes (Beaupre, 2002). The simulation represents interactions between environment (temperature, food availability), behavioral decisions (to forage or engage in reproductive activities), and physiological processes (digestion, *SDA*, metabolism, and growth). Each day of an individual's life is simulated, from birth until death or simulation end. Because the interactions among multiple bioenergetic variables can be represented simultaneously, the simulation provides an opportunity to investigate consequences of foraging mode and associated syndrome patterns on fitness responses such as growth, while holding other variables constant.

The reader is referred to the original model description for details on structure and specific subroutine contents (Beaupre, 2002). Here, we present a baseline simulation of an ambush forager and then modify program structure to represent an active forager. Prior to simulation for this chapter, we updated functions for the cost of digestion (*SDA*) to reflect new data available for *Crotalus horridus* ($SDA \text{ (ml CO}_2\text{)} = 12.158 \text{ } SW^{0.16} PW^{1.03}$, where *SW* is snake wet mass, and *PW* is prey wet mass), (Zaidan and Beaupre, 2003). The model takes as input an initial file of state variables (sex, age, *SVL*, wet mass, and stored energy) that represent a cohort of 30 neonate animals. Simulated individuals then forage and grow in a user-defined food environment represented by mean foraging success (*MFS*; the probability of capturing food on any given day in which foraging occurs), and a maximum size for available food items (in this case, 200 g wet mass). Figure 11.6 shows the mean 10-year growth trajectory ($n = 30$ replicates) of a typical ambush forager under conditions of 0.05 *MFS* (5% chance of capturing food on any given day). Note that the simulation produces a slow sigmoidal growth curve and a body size asymptote that represents an energetic balance between size-dependent maintenance (including activity) and mean energy intake.

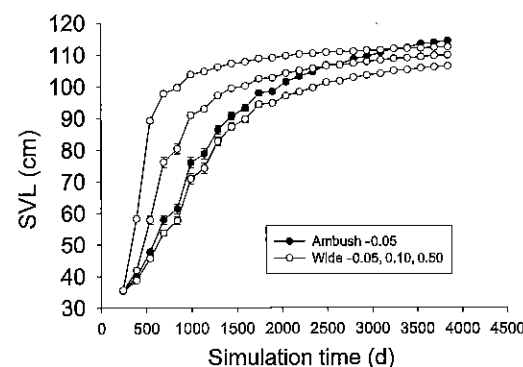


Figure 11.6. Simulated growth trajectories for ambush and active foragers. Mean foraging success (*MFS*) is defined as the probability of encountering prey on any day that foraging occurs. Note at similar *MFS*, ambush foragers grow more rapidly, and across most *MFS*, ambush foragers attain larger asymptotic body size (see text for details on simulation conditions and discussion).

We modified the simulation to represent an active forager by doubling *RMR* (which, because of sustained metabolic scope assumptions, resulted in a doubling of *FMR*) and by reducing total *SDA* by half. Whereas these factorial changes in energetic variables are broad and simplistic, they are not far removed from typical differences observed between active and ambush foragers (Secor and Nagy, 1994; Secor and Diamond, 2000). We then simulated an active forager under food availability conditions that were identical to those of the ambush forager (*MFS* = 0.05, maximum food size 200 g), and noted both decreased growth rate and smaller asymptotic body size relative to the ambush forager (Fig. 11.6). Furthermore, arbitrary increases in mean foraging success (*MFS* = 0.10, 0.50) for the active forager resulted in faster growth at small sizes, but had little effect on asymptotic body size (Fig. 11.6). Apparently, at small sizes, increased metabolism can easily be compensated for by increases in food availability. However, at large size, a doubling of metabolism effectively reduces asymptotic size even under conditions of abundant food. We believe this occurs because, even with abundant food, simulated snakes reach their maximum capacity to process (digestion takes time), forcing a lower equilibrium point for the trade-off between size-specific maintenance and net energy intake. Multiple simulations were conducted to explore the relation between physiological differences associated with foraging mode, food availability, and asymptotic body size (Fig. 11.7). Simulated ambush foragers attain larger asymptotic size than active foragers at any given food availability (Fig. 11.7) because their lower whole-body metabolic costs yield greater net energy for production. We note that in nature some of the largest

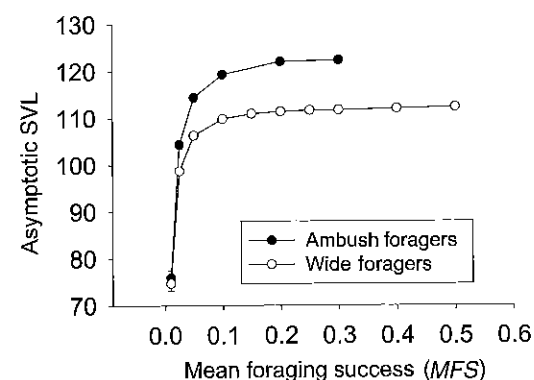


Figure 11.7. Simulated asymptotic body size for ambush and active foragers across a broad range of food availability and encounter rates (*MFS*). Under comparable *MFS*, ambush foraging snakes achieve greater asymptotic body size.

snakes can be found among ambush foraging lineages (i.e. Boidae, Pythonidae, Viperidae), although other factors such as the metabolic cost of transport clearly play an important role.

Our simulations are simplistic, especially in the sense that we have held all factors except *RMR*, *FMR*, *SDA*, and *MFS* equal. Nevertheless, the simulation results suggest that higher metabolic rates of active foragers must be compensated for by increased food capture rates or increased processing efficiency. The simulations have implications for the evolution of intermediate phenotypes between the ambush and active conditions. Clearly, departures from the tuned suite of characteristics for ambush foraging can only be supported under ecologically permissive circumstances (i.e. where food is predictable or abundant). Likewise, it seems unlikely that active foraging animals with high metabolic expenditures could easily switch to a more ambush foraging lifestyle without risking starvation. Simulation results support the perspective that, although foraging modes most likely range on a continuum between active and ambush, some points on the continuum (combinations of traits) are probably more difficult to achieve than others.

Closing remarks

In general, to the extent that available data allow responsible comparisons, snakes appear to follow the syndrome hypothesis in its coarsest form. However, during the preparation of this chapter, we became keenly aware of several problems with the uncritical application of the syndrome hypothesis to snakes. First, and perhaps foremost, a satisfactory and objective definition of

foraging mode in snakes is lacking. We were tempted to apply the simplistic definition that an active forager moves itself into striking range of prey, whereas an ambush forager waits until the prey enters striking range (McLaughlin, 1989; Perry, 1999); however, this dichotomy seems inadequate to account for dramatic differences in behavior, physiology and morphology associated with foraging mode in snakes (i.e. cost of movement, frequency of feeding). Likewise, definitions that quantify movement rates in relation to foraging are problematic in snakes, which are generally secretive and feed infrequently. Even ambush foraging snakes may move considerable distances in search of productive ambush sites (Duvall *et al.*, 1990). Greene (1997, pp. 62–6) eloquently discusses multiple exceptions and caveats among snakes that obviate the use of a simple dichotomous classification (ambush vs. active foragers). Furthermore, careful reading of detailed species accounts in taxonomic literature reveals remarkable flexibility in many snakes that shift foraging tactics during ontogeny, and in response to changes in food availability (Table 11.1). The plethora of snakes with apparently flexible foraging tactics defies their assignment into a simplistic dichotomy. Nevertheless, as documented by Fig. 11.2, 11.3, and 11.4, the foraging mode dichotomy appears to hold some predictive power relative to syndrome variables.

Second, the quality of data for comparison among snakes must be improved in several ways. The phylogenetic relationships of the Colubroidea need to be resolved into well-supported, defensible monophyletic groups. Researchers that measure syndrome-related variables should consider how the data may be used in comparative studies. Specifically, ratio data, such as *RCM* and mass-specific physiological rates, should be replaced with carefully estimated and well-sampled allometric relations. Finally, efforts should be made to incorporate data from taxa of more ambiguous foraging strategy (such as those in Table 11.1) and to study known reversals in greater detail.

We also perceive an unfortunate parallel between the syndrome hypothesis and “*r*- and *K*-selection” theory. Both approaches present dichotomous categories and list characteristics of organisms that guide their classification. However, most organisms do not fit cleanly into either category, rendering both classification schemes as non-mechanistic general models that explain no special cases (Dunham and Beaupre, 1998). Perhaps a more productive way to think about the consequences of foraging mode is to consider a multivariate suite of co-adapted traits (Arnold, 1983; Lande and Arnold, 1983). Ambush and active foraging may be local optima where more intermediate trait combinations are allowed only under permissive circumstances, such as predictable or abundant food. An exclusive focus on foraging mode as a causative factor driving behavior, physiology, and morphology is probably myopic. Foraging mode is correlated with

other forcing factors, such as feeding frequency, which may more directly influence the evolution of morphology and physiology (e.g. the regulation of gut function) (Secor, 2001) and selection for low-energy lifestyles, of which some snakes (e.g. rattlesnakes) may be extreme examples (Beaupre and Zaidan, 2001).

Finally, other large patterns in snake morphology may be related to foraging mode, including the evolution of caudal luring, macrophagy, and the evolution of crypsis. For example, ontogenetic shifts in morphology of the copperhead (see above) may be related to an ontogenetic shift from reliance on ambush caudal luring by neonates to more active foraging in the adult. Likewise, some extreme examples of macrophagy occur among ambush foraging snakes (Greene, 1992; Shine and Wall, this volume, Chapter 6). The evolution of macrophagy, and associated increases in viable prey size, is one possible solution to decreased energy input in infrequently feeding ambush foragers. Color pattern is also certain to shift in response to foraging mode. Widely foraging snakes with active lifestyles would benefit from coloration that enhances the use of "flicker fusion" to escape predation (Shine and Madsen, 1994; Lindell and Forsman, 1996), whereas ambush foragers would benefit from cryptic coloration that conceals them from predators and prey alike. The evolution of larger-scale patterns among snakes should enjoy greater attention as knowledge of phylogenetics and natural history increases within the group.

Acknowledgments

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Appendix 11.1 Data used in SMR comparisons
See text for details.

Species	n	Mode	Temp	b	a (J/h)	Mass (g)	SMR (V _{CO₂} or V _{O₂} /h)	SMR (J/h)	Log mass	Log SMR	Source	Reference
ACROCHORDIDAE												
<i>Acrochordus arafurae</i>	4	W	30	—	—	1048	24.7	485.3	3.02	2.69	table 1	Bedford and Christian, 1998
BOIDAE												
<i>Acrantophis dumerili</i>	7	A	30	0.62	7.57	2550	48.2	949.4	3.41	2.98	table 1	Chappell and Ellis, 1987
<i>Boa constrictor</i>	35	A	30	0.74	3.18	7825	126.1	2482.5	3.89	3.40	table 1	Chappell and Ellis, 1987
<i>Candoia carinatus</i>	14	A	30	0.71	2.41	525	50.5	205.7	2.72	2.31	table 1	Chappell and Ellis, 1987
<i>Corallus caninus</i>	7	A	30	0.88	1.12	550	14.6	287.6	2.74	2.46	table 1	Chappell and Ellis, 1987
<i>Corallus enhydris</i>	7	A	30	0.77	2.13	800	18.8	369.2	2.90	2.57	table 1	Chappell and Ellis, 1987
<i>Epicrates cenchria</i>	11	A	30	0.57	7.69	425	12.3	242.2	2.63	2.38	table 1	Chappell and Ellis, 1987
<i>Eryx colubrinus</i>	9	A	30	0.76	2.21	75	3.0	59.4	1.88	1.77	table 1	Chappell and Ellis, 1987
<i>Lichanura roseofusca</i>	6	A	30	—	—	314	22.0	432.6	2.50	2.64	fig. 1	Ruben, 1976
<i>Lichanura trivirgata</i>	12	A	30	0.66	3.79	175	5.9	116.2	2.24	2.07	table 1	Chappell and Ellis, 1987

Species	n	Mode	Temp	b	a (J/h)	Mass (g)	SMR		Log mass	Log SMR	Source	Reference
							(\dot{V}_{CO_2} or \dot{V}_{O_2} /h)	(J/h)				
COLUBRIDAE												
<i>Boiga irregularis</i>	5	W	30	—	—	133	5.4	149.4	2.13	2.17	table 1 (low 0-8)	Anderson <i>et al.</i> , 2003
<i>Coluber constrictor</i>	5	W	30	—	—	223	21.9	430.1	2.35	2.63	table 1	Secor and Diamond, 2000
<i>Coluber ravergieri</i>	5	W	30	—	—	136	7.9	155.5	2.13	2.19	fig. 2	Dm'el, 1972
<i>Diadophis punctatus</i>	10	W	30	1.02	2.62	5	0.6	12.4	0.66	1.09	table 2	Buikema and Armitage, 1969
<i>Helicops modestus</i>	34	W	30	0.59	9.60	100	7.2	142.1	2.00	2.15	table 1	Abe and Mendes, 1980
<i>Lampropeltis getula</i>	5	W	30	—	—	188	11.8	233.1	2.27	2.37	table 1	Secor and Diamond, 2000
<i>Liophis miliaris</i>	29	W	30	0.80	5.06	200	18.0	354.3	2.30	2.55	table 1	Abe and Mendes, 1980
<i>Malpolon moidensis</i>	10	W	30	—	—	145	11.5	225.4	2.16	2.35	table 1 (adults)	Al-Sadoon, 1991
<i>Masticophis flagellum</i>	11	W	30	—	—	124	5.5	108.7	2.09	2.04	p. 1606	Secor and Nagy, 1994
<i>Natrix maura</i>	7	A	30	—	—	25	2.0	39.4	1.40	1.60	table 2	Hailey and Davies, 1986
<i>Natrix n. helvetica</i>	5	W	30	—	—	100	13.0	255.2	2.00	2.41	table 2	Hailey and Davies, 1986
<i>Natrix n. persa</i>	7	W	30	—	—	40	2.9	56.3	1.60	1.75	table 2	Hailey and Davies, 1986
<i>Nerodia rhombifera</i>	20	W	30	—	—	250	21.4	420.7	2.40	2.62	p. 442	Jacobson and Whitford, 1970
<i>Nerodia sipedon</i>	10	W	30	—	—	292		873.6	2.47	2.94	table 4	Blem and Blem, 1990
<i>Nerodia taxipilota</i>	10	W	30	—	—	372		861.6	2.57	2.94	table 4	Blem and Blem, 1990
<i>Pituophis melanoleucus</i>	9	W	30	0.69	4.94	431	11.5	315.0	2.63	2.50	p. 453	Zaidan and Beaupre, 2003

<i>Spalerosophis diadema</i>	4	W	30	—	—	218	12.7	249.3	2.34	2.40	fig. 2	Dm'el, 1972
<i>Thamnophis proximus</i>	20	W	30	—	—	35	6.8	133.4	1.54	2.13	p. 442	Jacobson and Whitford, 1970
<i>Thamnophis sirtalis</i>	72	W	30	0.71	5.76	23	2.7	53.6	1.36	1.73	table 2	Peterson <i>et al.</i> , 1998
ELAPIDAE												
<i>Acanthophis praelongus</i>	3	A	30	—	—	106	5.0	99.2	2.02	2.00	table 1	Bedford and Christian, 1998
<i>Pseudonaja nuchalis</i>	3	W	30	—	—	214	14.4	283.4	2.33	2.45	table 1	Bedford and Christian, 1998
PYTHONIDAE												
<i>Antaresia childreui</i>	8	A	30	—	—	332	24.2	477.0	2.52	2.68	table 1	Bedford and Christian, 1998
<i>Antaresia stimsoni</i>	5	A	30	—	—	350	20.2	397.9	2.54	2.60	table 1	Bedford and Christian, 1998
<i>Aspidites melanocephalus</i>	3	A	30	—	—	1028	69.8	1473.6	3.01	3.17	table 1	Bedford and Christian, 1998
<i>Liasis fuscus</i>	4	A	30	—	—	1307	29.3	577.4	3.12	2.76	table 1	Bedford and Christian, 1998
<i>Liasis olivaceus</i>	5	A	30	—	—	3323	111.4	2192.7	3.52	3.34	table 1	Bedford and Christian, 1998
<i>Morelia spilota</i>	8	A	30	0.84	2.24	1050	37.9	746.0	3.02	2.87	table 1	Chappell and Ellis, 1987
<i>Python curtis</i>	8	A	30	0.86	1.09	2375	45.8	900.7	3.38	2.96	table 1	Chappell and Ellis, 1987
<i>Python molurus</i>	20	A	30	0.71	5.21	33950	455.0	8954.6	4.53	3.95	table 1	Chappell and Ellis, 1987
<i>Python regius</i>	53	A	30	—	—	1523	31.9	627.1	3.18	2.80	fig. 2A	Ellis and Chappell, 1987
<i>Python reticulatus</i>	15	A	30	0.75	4.93	14325	334.5	6582.8	4.16	3.82	table 1	Chappell and Ellis, 1987
<i>Python sebae</i>	10	A	30	0.76	3.68	16150	286.8	5644.3	4.21	3.75	table 1	Chappell and Ellis, 1987

Species	n	Mode	Temp	b	a (J/h)	Mass (g)	SMR (\dot{V}_{CO_2} or \dot{V}_{O_2} /h)	SMR (J/h)	Log mass	Log SMR	Source	Reference
VIPERIDAE												
<i>Agkistrodon piscivorus</i>	23	A	30	0.71	2.82	250	5.2	142.1	2.40	2.15	table 4, AR, EP	Zaidan, 2002
<i>Bothrops moojeni</i>	51	A	30	0.69	14.96	410	84.7	1655.8	2.61	3.22	table 2 (adults)	Cruz-Neto and Abe, 1994
<i>Cerastes cerastes</i>	10	A	30	—	—	121	8.6	169.1	2.08	2.23	table 1 (adults)	Al-Sadoon, 1991
<i>Crotalus adamanteus</i>	5	A	30	0.93	1.06	3373	102.8	2023.1	3.53	3.31	p. 148	Dorcas <i>et al.</i> , 2004
<i>Crotalus atrox</i>	41	S	30	0.66	4.17	300	9.1	179.8	2.48	2.26	—	S. Beaupre <i>et al.</i> , unpubl. data
<i>Crotalus cerastes</i>	16	A	30	—	—	129	4.0	78.7	2.11	1.90	p. 1606	Secor and Nagy, 1994
<i>Crotalus durissus</i>	15	A	30	—	—	50	2.2	43.3	1.70	1.64	p. 231	Cruz-Neto <i>et al.</i> , 1999
<i>Crotalus horridus</i>	36	A	30	0.78	2.00	300	6.1	168.4	2.48	2.23	table 4	Beaupre and Zaidan, 2001
<i>Crotalus lepidus</i>	16	A	30	0.60	2.87	115	2.5	69.0	2.06	1.84	table 3 F4, GVH	Beaupre, 1993
<i>Crotalus molossus</i>	16	A	30	0.60	2.87	300	4.5	122.6	2.48	2.09	table 3 F4, GVH	Beaupre, 1993
<i>Crotalus viridis</i>	6	A	30	—	—	301	24.1	473.9	2.48	2.68	fig. 1	Ruben, 1976
<i>Macrovipera palaestinae</i>	8	A	30	—	—	581	24.4	480.2	2.76	2.68	fig. 2	Dmi'el, 1972
<i>Vipera aspis</i>	8	A	32	—	—	85	4.3	83.6	1.93	1.92	table 3	Ladyman <i>et al.</i> , 2003
<i>Vipera berus</i>	10	A	30	—	—	70	9.5	186.0	1.85	2.27	table 1	Al-Sadoon, 1991

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